13 Noise, balanced feedback networks, synaptic scaling, and linear response. Part 2

13.1 Circuit model

So far we have only address noise and scaling at the level of noise in individual cells. Now we analyze a network of neurons with balanced inputs (Figure 1). We consider the consequences of the choice of connections in a network on the ability to maintain the balanced state.

Figure 1: Feedback circuit model with two populations of neurons

Consider a network of a population of interconnected excitatory (E) and inhibitory (I) cells. The full equations are

\[
\tau_E \frac{dV_i^E(t)}{dt} + V_i^E(t) = \left[ \beta (\mu_i^E(t) - \theta_i^E) \right]_+ \quad (13.1)
\]

and

\[
\tau_I \frac{dV_i^I(t)}{dt} + V_i^I(t) = \left[ \beta (\mu_i^I(t) - \theta_i^I) \right]_+ , \quad (13.2)
\]

where \([ \cdot \cdot \cdot ]_+\) is the Heavyside function, \(\tau_E\) and \(\tau_I\) are the cellular time constant, \(\beta\) is the conversion gain, and the \(\theta_i^E\) and \(\theta_i^I\) are
thresholds. The inputs are

$$\mu^E_i(t) = \mu^{E}_{ext}(t) + \sum_{j=1}^{K} W_{ij}^{EE} V^E_j(t) + \sum_{j=1}^{K} W_{ij}^{EI} V^I_j(t)$$  \hspace{1cm} (13.3)$$

and

$$\mu^I_i(t) = \mu^{I}_{ext}(t) + \sum_{j=1}^{K} W_{ij}^{II} V^I_j(t) + \sum_{j=1}^{K} W_{ij}^{IE} V^E_j(t).$$  \hspace{1cm} (13.4)$$

As in the case of the model cell, we will scale the synaptic inputs by $1/\sqrt{K}$, as opposed to $1/K$, i.e.,

$$W_{ij}^{EE} \rightarrow \frac{W_{ij}^{EE}}{\sqrt{K}}; \quad W_{ij}^{II} \rightarrow -\frac{W_{ij}^{II}}{\sqrt{K}}; \quad W_{ij}^{EI} \rightarrow -\frac{W_{ij}^{EI}}{\sqrt{K}}; \quad W_{ij}^{IE} \rightarrow \frac{W_{ij}^{IE}}{\sqrt{K}}$$  \hspace{1cm} (13.5)$$

where we explicitly put in the negative signs of inhibition. As will soon be clear, we need to scale the external inputs by

$$\mu^{E}_{ext}(t) \rightarrow \sqrt{K} E m_{ext}(t) \quad \text{and} \quad \mu^{I}_{ext}(t) \rightarrow \sqrt{K} I m_{ext}(t)$$  \hspace{1cm} (13.6)$$

where $E$ and $I$ are inputs of strength of $O(1)$. The dependence on a common term is a statement that excitatory and inhibitory neurons share the same tuning curve. All together, we have

$$\mu^E_i(t) = \sqrt{K} E m_{ext}(t) + \frac{W_{ij}^{EE}}{\sqrt{K}} \sum_{j=1}^{K} V^E_j(t) - \frac{W_{ij}^{EI}}{\sqrt{K}} \sum_{j=1}^{K} V^I_j(t)$$  \hspace{1cm} (13.7)$$

and

$$\mu^I_i(t) = \sqrt{K} I m_{ext}(t) + \frac{W_{ij}^{IE}}{\sqrt{K}} \sum_{j=1}^{K} V^E_j(t) - \frac{W_{ij}^{II}}{\sqrt{K}} \sum_{j=1}^{K} V^I_j(t).$$  \hspace{1cm} (13.8)$$

In terms of the order parameters,

$$\mu^E(t) = \sqrt{K} E m_{ext}(t) + \sqrt{K} W_{ij}^{EE} \frac{1}{K} \sum_{j=1}^{K} V^E_j(t) - \sqrt{K} W_{ij}^{EI} \frac{1}{K} \sum_{j=1}^{K} V^I_j(t)$$

$$= \sqrt{K} E m_{ext}(t) + \sqrt{K} W_{ij}^{EE} m_E(t) - \sqrt{K} W_{ij}^{EI} m_I(t)$$

$$= \sqrt{K} \left[ E m_{ext}(t) + W_{ij}^{EE} m_E(t) - W_{ij}^{EI} m_I(t) \right] \hspace{1cm} (13.9)$$

and

$$\mu^I(t) = \sqrt{K} I m_{ext}(t) + \sqrt{K} W_{ij}^{IE} \frac{1}{K} \sum_{j=1}^{K} V^E_j(t) - \sqrt{K} W_{ij}^{II} \frac{1}{K} \sum_{j=1}^{K} V^I_j(t)$$

$$= \sqrt{K} \left[ I m_{ext}(t) + W_{ij}^{IE} m_E(t) - W_{ij}^{II} m_I(t) \right].$$  \hspace{1cm} (13.10)$$
As $\sqrt{K} \to \infty$ the left hand side goes to zero and the equilibrium state will satisfy

$$0 \left( \frac{1}{\sqrt{K}} \right) = E m_{ext}(t) + W^{EE} m_E(t) - W^{EI} m_I(t) \quad (13.11)$$

and

$$0 \left( \frac{1}{\sqrt{K}} \right) = I m_{ext}(t) + W^{IE} m_E(t) - W^{II} m_I(t). \quad (13.12)$$

The implication of this equilibrium condition is that the average input remains finite as the fluctuations remain large (Figures 2 and 3). This is the balanced state.

**Figure 2:** Balanced networks have emergent variability. From Shadlen and Newsome, 1994.

![Figure 2](image)

**Figure 3:** Statistics of have emergent variability. From Shadlen and Newsome, 1994.

![Figure 3](image)

### 13.2 The balanced state

Solving the above equations for $m_E^0$ and $m_I^0$ gives relations for the equilibrium activity of the excitatory and inhibitory cells in terms of the external drive:

$$m_E^0 = \frac{W^{II} E - W^{EI} I}{W^{EE} W^{II} - W^{EI} W^{IE}} m_{ext}. \quad (13.13)$$
and
\[ m_I^0 = \frac{W_{IIE} - W_{IEI}}{W_{IEI}W_{IIE} - W_{EIW_{IE}}} m_{ext}. \] (13.14)

Recall that the equilibrium values of activity \( m_E^0 \) and \( m_I^0 \) must be both positive and bounded by 1. This constrains the values of the synaptic weights.

### 13.2.1 Linear response

A seemingly paradoxical effect is that increasing the external inhibitory input, i.e., increasing \( I \), will lead to a net decreased spiking of inhibitory cells and will concurrently decrease both \( m_E \) and \( m_I \) (Figure 4). This is a feedback effect. Excitatory and inhibitory activity track each other until the excitatory cells are completely turned off; this behavior is seen across cortical regions (Figure 5).

**Figure 4:** Experimental set-up to study linear response of network as we drive inhibition. From Sanzeni, Akitake, Goldbach, Leedy, Brunel and Histed 2020.

**Figure 5:** Linear response, until saturation, of network as we drive inhibition. From Sanzeni, Akitake, Goldbach, Leedy, Brunel and Histed 2020.
A second issue is that rapid feedback prevents the occurrence of significant correlations. This depends on having faster inhibitory than excitatory synapses, as occurs for Gaba-A, but not Gaba-B (Figure ??).

### 13.2.2 Stability and response speed

We return to the full network equations and look at the variation around the equilibrium value of $m_E$ and $m_I$. Taking the time constants, $\tau$, conversion gains, $\beta$, and thresholds to be the same for the $E$ and $I$ populations, and denoting

$$\delta m_E(t) = m_E(t) - m_E^0$$

and

$$\delta m_I(t) = m_I(t) - m_I^0$$

leads to

$$\tau \frac{d}{dt} \delta m_E(t) + \delta m_E(t) = \left[ \beta \sqrt{K} \left( W_{EE} \delta m_E(t) - W_{EI} \delta m_I(t) \right) \right]_+$$

(13.17)

and

$$\tau \frac{d}{dt} \delta m_I(t) + \delta m_I(t) = \left[ \beta \sqrt{K} \left( W_{IE} \delta m_E(t) - W_{II} \delta m_I(t) \right) \right]_+.$$  

(13.18)

When the neurons are active, this reduces to the linear equations

$$\tau \frac{d}{dt} \delta m_E(t) + \delta m_E(t) = \beta \sqrt{K} \left( W_{EE} \delta m_E(t) - W_{EI} \delta m_I(t) \right)$$

(13.19)

and

$$\tau \frac{d}{dt} \delta m_I(t) + \delta m_I(t) = \beta \sqrt{K} \left( W_{IE} \delta m_E(t) - W_{II} \delta m_I(t) \right).$$

(13.20)

These linear equations are solved by taking $\delta m(t) \propto e^{\lambda t}$, so that

$$(\lambda \tau + 1) \delta m_E(t) = \beta \sqrt{K} \left( W_{EE} \delta m_E(t) - W_{EI} \delta m_I(t) \right)$$

(13.21)

and

$$(\lambda \tau + 1) \delta m_I(t) = \beta \sqrt{K} \left( W_{IE} \delta m_E(t) - W_{II} \delta m_I(t) \right),$$

(13.22)

which requires that

$$\begin{vmatrix} \beta \sqrt{K} W_{EE} - 1 - \lambda \tau & -\beta \sqrt{K} W_{EI} \\ \beta \sqrt{K} W_{IE} & -\beta \sqrt{K} W_{II} - 1 - \lambda \tau \end{vmatrix} = 0$$

(13.23)
and leads to

\[
\lambda_{1,2} = \frac{\beta \sqrt{K} (W^{EE} - W^{II}) - 2}{2\tau} 
\]

\[
\pm \frac{1}{\tau} \sqrt{\left(\frac{\beta \sqrt{K} (W^{EE} - W^{II}) - 2}{2}\right)^2 - \beta^2 K W^{IE} W^{EI}} 
\]

\[
K \to \infty \quad \frac{\beta \sqrt{K}}{\tau} \left[ \frac{W^{EE} - W^{II}}{2} \pm \sqrt{\left(\frac{W^{EE} - W^{II}}{2}\right)^2 - W^{IE} W^{EI}} \right] 
\]

\[
\frac{\beta \sqrt{K}}{\tau} \left[ \frac{W^{EE} - W^{II}}{2} \right] \left[ 1 \pm \sqrt{1 - 4 \frac{W^{IE} W^{EI}}{(W^{EE} - W^{II})^2}} \right]. 
\]

The system is stable only if the real part of $\lambda_{1,2} < 0$. This implies

\[
W^{II} > W^{EE}, \quad (13.25)
\]

which is a prediction for connectomic analysis. We note that, by construction, $W^{IE} W^{EI} > 0$. The response time of the system is shortened by a factor of $\sqrt{K}$, i.e.,

\[
\frac{\tau}{\beta} \to \frac{\tau}{\beta \sqrt{K} O(1)}. \quad (13.26)
\]

The change in recovery speed of the network has not been properly measured. But a sudden jump in the excitation of cortical input leads to an observed time-constant of about 10 ms (Figure 6). Unfortunately this is not very different from estimates for isolated neurons and thus the dynamics of the balanced still is a topic under analysis.

**Figure 6:** Relaxation of the signal in V1 cortical neurons after shut-down of thalamus. From Reinhold, Lien and Scanziani 2015